ON THE PRIMITIVE REPTILE PROCOLOPHON.

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(Text-figures 30–38.)

The Types of Procolophon.—The two specimens on which Sir R. Owen founded the genus *Procolophon* in 1876 are in the British Museum of Natural History. The author was uncertain as to the value of the characters in which *P. minor* differs from *P. trigoniceps*, intimating that it may be a young example of that species. The skulls seem to differ in their proportions (text-figs. 30 and 31). *P. minor* (text-fig. 30) is relatively broader, having the width to length of the skull as 5 to 4. In *P. minor* the orbits are more distinctly ovate, and placed further forward, being in the middle

Text-fig. 30.

Type specimen of *Procolophon minor*, from Donnybrook [the sutures are not so distinct in the specimen as in the figure].

third of the length of the head, in advance of the parietal foramen and scarcely extending behind the lateral borders of the frontal bones; the region in advance of the orbits is relatively short; the quadrate has no expansion backward as in other specimens; there is no trace of a foramen in the malar arch. Neither fossil gives conclusive evidence of the form of the teeth. Though they are in both types described as conical and pointed, it is not possible to determine the form of the crown when the jaws are closed, as is

evident in *Trirachodon* and other genera. The differences between the two specimens may be found to justify generic separation.

The Quadrate Bone.—The most striking difference is in the character of the bone which articulates with the mandible (text-figs. 30, 31). In *P. minor* the quadrate bone is partly imbedded in matrix, so that there is no reason to suppose that any structure is lost from that region. The quadrate bone is directed downward and backward, is compressed from front to back, forms a transverse articulation, somewhat constricted in the middle, and is thickened on the lateral external surface above the articulation ; but the bone shows no indication of the posterior development which was named squamosal by Sir R. Owen, and afterward regarded as probably quadrato-jugal by myself, which is so well developed in *P. trigoniceps* (text-fig. 31). A fresh examination of these and other skulls leads me to remark that the place of the quadrato-jugal bone is between the malar bone and the quadrate, but there is no ossification in that position in *Procolophon*. Therefore I infer that the quadrato-jugal bone has no existence in *Procolophon*. The thick cellular bone which extends from the jugal behind the articulation I am unable to separate from the quadrate bone, which articulates with the mandible, since no specimen shows a dividing suture between it and the bone which articulates with the mandible. This determination, if sustained, removes the anomaly of the quadrato-jugal attaining an enormous thickness. Its supposed position behind the malar and external to the quadrate was paralleled by the thin quadrato-jugal in *Ichthyosaurus*.

The Parietal Region.—The region behind the frontal bones and orbits, which is commonly termed parietal, shows faint obscure markings in *P. minor* (text-fig. 30) of lines in a transverse curve from the bone named epiotic to the hinder border of the parietal foramen, and short longitudinal lines prolonging the inner and outer borders of the orbits backward. The latter led me formerly to suppose that the postfrontal occupies a quadrate area in front of the epiotic extending forward to the orbit. The only other specimen in which the parietal region appears to be divided in similar way by faint markings is the British Museum skull R. 1999. The parietal bone is composite in *Mochlorhinus* and other genera. But while the appearances in *Procolophon* may be due to squamous overlap of bones, the evidence is insufficient to establish their nature, though it strongly suggests the structure in some Labyrinthodont skulls.

The Postsquamosal Bone.—The bone which is found at the posterior external angle of the flat parietal region I have formerly referred to as the epiotic. It corresponds in position with the bone so named in Labyrinthodonts, though, as most writers on Labyrinthodonts have remarked, it has nothing in common with the otic bone named epiotic by T. H. Huxley. This ossification is named squamosal by Dr. A. S. Woodward in his 'Vertebrate Palæontology,' but it is a thin plate of bone, quite distinct from the squamosal and superimposed upon it. If the

markings already referred to, which appear to indicate a posterior division of the parietal bones, really indicate bones, they would represent the pair of ossifications termed supraoccipital in Labyrinthodonts, over which the parietal bones may extend. *Procolophon* may thus far be crypto-Labyrinthodont in the structure of this part of the head. In *Pareiasaurus* there appears to be a narrow bone behind the parietal bones (Phil. Trans. Royal Soc. 1888, p. 69) and also a pair of bones behind the squamosals, postsquamosal bones as they may be named, which are in the position of the bones previously termed epiotic. The preservation in *Pareiasaurus* of this region of the skull leaves much to be desired, but it suggests comparison with *Procolophon*.

Text-fig. 31.

Type specimen of *Procolophon trigoniceps*, from Donnybrook. For comparison with *P. minor*.

The Postorbital bar.—The preservation of the type of *Procolophon trigoniceps* (text-fig. 31) is not quite satisfactory, owing to cranial bones having scaled off from the frontal region and the postorbital area on the right side. On the left side there appears to be a slight, almost imperceptible linear separation between the postorbital and the squamosal and quadrate bones. It might pass as a condition of fossilization, since it is absent in *P. minor*, but for the circumstance that the condition becomes a foramen in *P. laticeps* (text-fig. 32). There is no trace of the slit on the right side of the skull. There the sutural lines indicate a long narrow strip of bone descending

below the postsquamosal above, and between the squamosal and quadrate bones behind it and the postorbital in front, so that the space between the bones, which might be occupied by the supratemporal, has only a linear extension on the external surface, above the malar. The internal suture which separates a supratemporal from the squamosal is not clear in specimens of other species.

The Postfrontal.—One of the most characteristic features of *Procolophon* is the small size of the postfrontal bone, which is a narrow strip above the orbit external to the parietal and frontal, contrasting with the relatively large size of the prefrontal bone. There is an appearance of the prefrontal and postfrontal both underlapping the frontal bones in *P. trigoniceps*, but the preservation is dissimilar on the right and left side of the head, and the evidence is not conclusive that the postfrontal is larger than it appears to be. This character is in marked contrast to the condition in Dicynodontia and Theriodontia, in which the postfrontal not only contributes to the bar which divides the orbit from the temporal vacuity, but is prolonged backward on the temporal vacuity along the bevelled margin of the parietal bone.

I conclude, from detailed comparison of these structures and from measurements, that the type species are founded upon characters which clearly distinguish them. Other evidence shows unexpected variation in the skulls *of Procolophon*.

In 1878 I described additional material also from Donnybrook, and discussed the affinities of the genus with *Hatteria* and Anomodont reptiles. Three species appeared to be indicated by as many specimens, and were described under the names *P. griersoni*, *P. laticeps*, and *P. cuneiceps*, and figured in pl. xxxii. Quarterly Journal Geol. Soc. vol. xxxiv. The matrix was afterwards further removed from these fossils, chiefly in the endeavour to elucidate the back of the skull and the quadrate region. The published figures, which are somewhat rough, are chiefly directed to show external variations of form, and the divided nares. Beyond correcting the identification of the postfrontal bone in the way already indicated in the evidence figured in 1889 (Phil. Trans. Roy. Soc. B. pl. 19), and omitting the quadrato-jugal bone, I have nothing to modify in those descriptions; but better specimens would be required to prove that the characters in which they differ are constant.

The Occipital Region.—Although all these types were developed to display the occipital region, it was only found in *Procolophon laticeps*. The transverse, slightly concave occipital border of the roof of the skull, formed by the parietal bones and postsquamosal bones at the outer angles (text-fig. 31), extends backward as a ledge beyond the nearly vertical occipital aspect of the skull, which it slightly overhangs. The ledge is inclined downward, and terminates in a sharp edge, which at the outer angles curves down with the postsquamosal to form an arch above the auditory notch behind the squamosal bone (text-fig. 32).

Quadrato-squamosal Arch.—The squamosal bone, which occupies a small area on the lateral aspect of the skull between the post-squamosal above and the quadrate bone below, is better seen on the occipital aspect (text-fig. 32), where it forms the upper and narrower part of the quadrato-squamosal pedicle for articulation with the mandible. The pedicle is nearly vertical, being inclined slightly backward as it extends downward, is convex on the straight side, and concave on the outer part, where the portion regarded hitherto as the quadrato-jugal is prolonged behind this surface outward and backward. The posterior aspect of the pedicle is crossed obliquely in its middle part by the sagittate suture which divides the squamosal bone from the quadrate, so that, passing downward and inward, it does not reach the mandibular articulation, which is formed by the quadrate bone. The height to the roof of the skull is $\frac{8}{10}$ inch. The transverse width of the quadrate bone at the articulation is about half an inch. This is exclusive of the great internal process of quadrate contour which extends inward and forward above the infra-quadrate process of the pterygoid bone, and internal to the descending process of the squamosal, and is exposed in one skull by removing the occipital bones.

The occipital surface of the skull, properly so called, is entirely behind the squamoso-quadrate region. Its vertical measurement is about half an inch, and the transverse width about an inch and a quarter. Below the postsquamosal bones its contour inclines to be transversely fusiform, owing to the inferior median basi-occipital convexity and the lateral concave inferior emargination below the opisthotic bones (text-fig. 32).

The foramen magnum occupies the middle of the area. It is higher than wide, wider below than above, margined laterally by an elevated rounded border, such as might possibly have carried a pro-atlas. Inferiorly this border merges in the occipital condyles, which are defined by a median concavity. The sutures are not distinct, but the basioccipital appears to enter into this median concavity, so that the two condyles from which the bony tissue has been rubbed are upon the exoccipital bones. Above the condyles a transverse horizontal suture separates the exoccipital from the supraoccipital bones, which are larger. Externally these bones are limited by a vertical suture, which separates them from the opisthotic, which is subtriangular and terminates outward in a blunt process below the postsquamosal and slightly in advance of it. There may be an interparietal above the supraoccipital bones and below the parietal. The flattened surfaces of these bones appear a little concave, owing to the elevation of the border of the foramen magnum. The distinctive character of this region is the closed occiput, which is more like that of *Crocodilus* than *Testudo*, and if the quadrate bones of a Crocodile were directed downward instead of backward, the occipital region of the skull would be more closely comparable with *Procolophon* in its backward extension and elevation above the mandibular articulation. The only South African reptile which approximates to this

relation of the occipital and quadrate regions is *Pareiasaurus*; but the large lateral perforations in the occiput and single condyle for the occipital articulation prevent close comparison with *Procolophon*. There is a similar approximation to the condition in some Labyrinthodonts in this relation of the two parts of the occipital region, but in most of those types the occipital plate inclines obliquely forward, and is not comparable in the details of structure of the skull. In no Dicynodon or Theriodont is there any approximation to *Procolophon* in this region of the skull, except in the occipital plate being usually imperforate.

Text-fig. 32.

Type specimen of *Procolophon laticeps*, from Donnybrook, showing (*a*) the vertical occipital plate and (*b*) the postorbital foramen.

The specimen figured in 1889 (Phil. Trans. pl. 9) as *Procolophon trigoniceps* was thus identified, as I now think, in error, because the matrix was not then removed from *P. laticeps*. From its excellent preservation Dr. Exton's fossil has been referred to as the type of *Procolophon*. That skull is exceptional in showing a distinct lateral postorbital foramen between the squamosal, postorbital, and malar bones. When originally described, the vacuity was regarded as being in the position of the supra-temporal bone, which was supposed to have disappeared as in Crocodiles, leaving a postorbital vacuity. Dr. Smith Woodward speaks of it (Verteb. Palæont. p. 148) as evidently the beginning of a lateral temporal vacuity, and this view is adopted by Prof. Osborn (Mem. Amer. Mus. vol. viii. p. 480). Whatever may be the value of the character, it is absent from Owen's types, as already remarked. It is only found among described species in *P. laticeps*,

where the foramen is distinct, ovate, and larger (on the left side of the head), and is between the malar, postorbital, squamosal, and quadrate. It is a linear gap in the bones in one specimen. It is much smaller than the vacuity in the side of the skull in *Palæohatteria*. The extension of the foramen downward to the quadrate bone involves no substantial difference from the British Museum specimen R. 1999, so that the name *Procolophon laticeps* may be used for that specimen, in preference to *P. trigoniceps* used in Phil. Trans. 1889, pl. 9.

The Teeth.—Usually the mandible is in close contact with the skull, so that the teeth are not seen, except on their external or internal aspects. The incisors are rather longer and stouter in aspect than the maxillary or molar teeth. They are conical, but flattened on the inner surface, which carries a few vertical ridges. I have failed to obtain evidence of implantation in sockets by making a vertical section.

Text-fig. 33.

Palate of *Procolophon cuneiceps*, showing the molar teeth; from Donnybrook.

A specimen in the British Museum, R. 794, was developed in fruitless search for the occiput, but now shows with exceptional clearness the structure of the quadrate region and the palate (text-fig. 33). The pterygoids and vomera are shown bearing teeth, the palatine bones, palatine plates of the maxillary bones, and the maxillary are seen on the palate. The most interesting feature of the dentition is the crowns of the maxillary teeth, which unexpectedly have a transverse molar form, as in the lizard *Tejus*. They are six in number on each side, wide transversely, with distinct inner and outer cusps, and with the inner and outer triturating surfaces separated by interspaces which appear to have received

the molar teeth of the mandible, which have not yet been examined. All the teeth contain large pulp-cavities, which extend into the cusps of the crowns. This type of dentition, notwithstanding the suppression of the functional canine teeth, as in *Microgomphodon*, is perhaps more like that of existing lizards than of Theriodonts, though there is a distinct resemblance to the teeth of some South-African Theriodont fossils, and the skull as a whole is not Lacertilian.

Forms of Skull.—Dr. Schönland in 1895 submitted to me a series of casts of specimens of *Procolophon* in the Albany Museum, Grahamstown, obtained by Messrs. A. E. and H. Trollip, of Fernrocks. He subsequently brought the original specimens to the British Museum, and gave me the opportunity of taking a series of impressions of the more important of them. Figures were prepared and the following notes drafted on these materials. A brief catalogue of the specimens was published by Dr. R. Broom, in 1903, in the 'Records of the Albany Museum,' vol. i. part 1, pp. 8–24, all the specimens being referred to *Procolophon trigoniceps*. Three specimens are figured by him. Among the casts are remains of a species of *Petrophryne*, which need to be carefully separated.

Text-fig. 34.

Impression of a palate of *Procolophon*, showing crowns of the molar teeth; from Fernrocks.

The Fernrocks specimens appear to be referable to different species from those collected at Donnybrook. Dr. Broom finds but three teeth in each premaxillary, and in some specimens from Donnybrook there are four premaxillary teeth. In the British Museum specimen R. 794 (text-fig. 33, p. 224), which is the only Donnybrook specimen showing the entire palate, the palatal suture between the premaxillary and maxillary bones appears to be transverse and in advance of the first pair of maxillary teeth, which are level with the small group of palatal teeth at the anterior extremity of the vomerine bones. In the Fernrocks cast of the

palate (text-fig. 34, p. 225), which Dr. Sehönland numbered 1, the premaxillary bones extend backward in a wedge between the maxillary bones, so that the vomerine teeth are behind the middle of the maxillary teeth. The vomerine teeth, instead of covering the vomera as in *P. laticeps*, or forming a close-set group as in R. 794, *P. cuneiceps*, diverge backward in two rows from two strong teeth in front separated by a well-marked median groove. There are five or six teeth in each row. Internal to these are parallel shorter rows, which similarly begin with two stronger teeth in front. Further, in the Donnybrook specimen the pterygoid bones separate in an arch (text-fig. 33, p. 224) which is three-fourths of a circle, round which there is a semicircular row of small teeth. But in the Fernrocks palate this median vacuity is bordered by a pair of prominent ridges which diverge backward in a V-shape, each carrying six or seven teeth. These rows are flanked laterally by parallel rows of teeth, which complete the form of a letter M (text-fig. 34). The lateral rows appear to be upon the palatine bones.

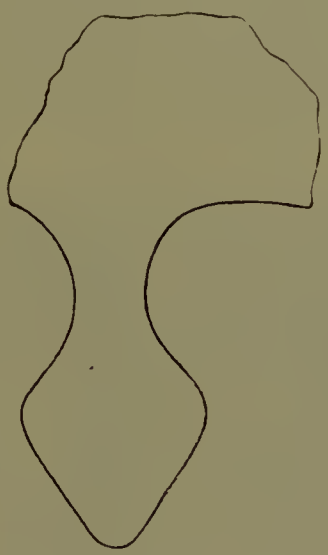
Text-fig. 35.

Outline showing the truncated snout of *Procolophon platyrhinus*, from Fernrocks.

The other examples of skulls which have come into my hands from Fernrocks, such as those numbered by Dr. Sehönland 2, 12, 13, all differ from the Donnybrook specimens in having the preorbital region of the skull much wider and flatter above, without any indication of the tapering conical snout which is found in all the described species. This character (text-fig. 35) may be conveniently expressed in the name *Procolophon platyrhinus* for the flat-nosed species, with the region of the nasal bones forming a flattened truncated prolongation of the frontal region, with the postorbital region long and wide. A longer flat preorbital region is seen in another skull (text-fig. 36). If referable to *Procolophon*, it may be named *P. sphenorhinus*, terminating in a vertical wedge in front.

There are many differences from the types of *Procolophon* in other parts of the skeleton, which suggest that the Fernrocks specimens may belong to a different genus; and there are certainly two species from Fernrocks.

Text-fig. 36.



Outline showing the wedge-shaped snout of *Procolophon sphenorhinus*, from Fernrocks.

Pelvis.—The form of the ilium is partly shown in the figure of the Donnybrook skeleton. Dr. R. Broom has figured the pubes and ischia (Rec. Alb. Mus. vol. i. pl. 1. fig. 5) from Fernrocks. The evidence that those bones belong to *Procolophon* is supplied by the proximal end of the femur, which shows substantially the same characters as the specimen from Donnybrook, figured in the Phil. Trans. Royal Soc. in 1889. It is associated with dorsal vertebræ with small intercentra and a median longitudinal groove on the ventral aspect; with caudal vertebræ rounded on the ventral aspect carrying ribs which extend transversely beyond the ischia. The ilia are less clearly seen than in the original slab. The chief characters of this pelvis are the foramen perforating the pubis, the antero-posterior extension of the crest of the ilium, and the expanded forms of the short pubes and longer ischia. In form these ventral bones of the pelvic basin differ from Theriodonts like *Cynognathus* in the absence of an obturator foramen, though there is a small semicircular notch on the anterior border of a right ischium. The perforation of the pubic bone is a character of *Pareiasaurus* and of other large undescribed genera in which I have seen the bone in the South-African veldt. It also occurs in *Phocosaurus* and *Titanosuchus*. The character is not seen in *Microgomphodon*, in which the ischium is similar in form.

The bones have a general resemblance in outline to the Pliosaurian type and to some Triassic Ichthyosaurs, but in neither is the pubic bone perforated. In the Trias of Europe the nearest parallel is found, perhaps, in the Neusticosauridæ, though, according to Volz, the pubis and ischium in that type had no linear contact as in the Pareiasauria. There is a general approximation to the forms of the bones in the pelvis of *Palæohatteria*, as indicated by Dr. R. Broom, and this is as close as in *Pliosaurus*, but the pubis is notched on its hinder border, and not perforated as in *Procolophon*. The *Stereosternum tumidum* of South

Text-fig. 37.

a *b* *c*

Hind limbs of *Procolophon*, from Fernrocks.

a, femur and tibia from the front; *b*, entire hind limb, posterior aspect; *c*, side view of the femur.

America is the only genus which exactly parallels *Procolophon* in the pelvis. It is nearer than *Mesosaurus*. Neither of these genera admits of comparison in the occipital region of the skull. But the pelvic identity of structure may justify the reception within the Procolophonia of these allied types, although they have been placed in distinct orders.

Femur.— The femur of *Procolophon* from Fernrocks is well shown

in the imperfect example which adjoins the pelvis. Its proximal end is about intermediate in form between the femur in a Chelonian and in *Ornithorhynchus*; for the under surface of the articular head is a wide concave pit (text-fig. 37, *b*), not without suggestion of the bone in *Saurodesmus* and the small mammal from Stonesfield and certain birds. The trochanters on each side of the articular head are much less developed than in the Monotreme, and the subarticular pit is less conspicuous in the other specimens from Fernrocks than in the Donnybrook example, which may indicate other species. The bone can best be compared with Pareiasauria. The external or posterior trochanter is produced down the shaft as a slight ridge on the under side of the bone in one specimen. The triangular section of the shaft is not so marked as in the Donnybrook specimen, and the proximal end is more flattened on the superior or anterior surface (text-fig. 37, *a*). The curvature of the bone is distinctly sigmoid in length (text-fig. 37, *c*). Distally it both thickens and widens to the articulation, where it is flattened on the inner side, concave behind, with a pulley articulation in front. One femur is longer and another shorter than the common type. There is no living reptile to which the bone approximates.

Tibia and Fibula.—The tibia is much stouter than the fibula. Its proximal end is triangular, being flattened behind, more like the tibia of a mammal than of a Dinosaur. Its wide proximal end forms the larger part of the articulation with the femur. The bone is about $\frac{6}{7}$ of the length of the femur (text-fig. 37, *b*).

Text-fig. 38.

Humerus and adjacent bones of fore limb, from Fernrocks.

The Fore Limb.—The fore limb was relatively small in the *Procolophon laticeps* (Phil. Trans. 1889, pl. 9). The humerus is considerably expanded at the proximal end, with a large radial crest, and manifestly twisted in the shaft, much as in *Aristodesmus* and in many of the Anomodontia. But the distal end is

not exposed. Among the materials for which I am indebted to Dr. Schönland is a slab (showing no conclusive evidence of the characters of *Procolophon*) with remains of vertebræ and ribs of a young animal, in which the humerus, ulna and radius, and scattered bones of the extremity are preserved. The proximal end of the humerus is but little seen, the shaft is twisted, and the distal end of the bone expanded as in Anomodonts, with a large entepicondylar foramen, and on this side of the distal articulation the bone is rounded in contour as in Dicynodonts.

The ulna and radius are slightly shifted in position, but are parallel bones which are shorter than the humerus. I suppose the bone which is stouter proximally to be the ulna, and that the slender bone is the radius, which appears to widen distally.

Conclusion.

The evidence from all parts of the skeleton points towards similar conclusions. The skull, with its general affinity with Anomodont reptiles, comes closer to the Pareiasauria in the relation of the quadrate region to the back of the head, and closer to the Theriodonts in dentition. The shoulder-girdle is also suggestive of the Pareiasauria, but the permanent separation of all the bones and the great anterior development of the pre-coracoid are distinctive characters. There is a similar affinity in the pelvis and in the hind limb and fore limb, but the differences point in all cases to a relation with groups which have Labyrinthodont affinities. The evidence is too imperfect to justify a final determination of relationship with all the Permian and Triassic Reptilia, but it sustains the conclusion that the order Procolophonia was based upon substantial differences of this type from its allies.